

Heterospecific shoaling in an invasive poeciliid: shared history does not affect shoal cohesion

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1 **ABSTRACT**

2 Social behaviour potentially plays an important role in invasion success. New colonists, for example,
3 may glean useful information about predators and food by interacting with native heterospecifics.
4 The extent to which invaders benefit from such social interactions could hinge on their prior
5 exposure to other species. Here we ask how the shoaling decisions of the Trinidadian guppy, *Poecilia*
6 *reticulata*, - a successful invasive species - are mediated by their shared history with a heterospecific,
7 the phenotypically similar *Micropoecilia picta*. To do this, we monitored shoal cohesion in single-
8 species treatments and in treatments where *M. picta* was present. We predicted that shoal cohesion
9 would be greater in single than in mixed species shoals. We also hypothesised that mixed species
10 shoals consisting of fish with a shared history would be more cohesive than those where the two
11 species had hitherto occurred allopatrically. We found that shoal cohesion did not differ between
12 single and two-species treatments, or in relation to shared history with *M. picta*. However, we also
13 discovered that while guppies were more often found in mixed-species than single-species shoals,
14 they were more likely to have a conspecific individual as their nearest neighbour within mixed-
15 species shoals. These results show that guppies willingly shoal with heterospecifics, even in the
16 absence of a shared history, but also reveal that the resulting shoals are not randomly assembled.
17 This flexibility in shoaling may confer a crucial advantage in the initial stages of invasion.

18 **Keywords:** guppy, invasive species, *Poecilia reticulata*, shoal cohesion, shoaling, social behaviour

19 **INTRODUCTION**

20 Groups of fish that remain together for social reasons are defined as shoals (Kennedy & Pitcher,
21 1975; Pitcher, 1983) and it is in this context in which most social learning – the acquisition of skills
22 and knowledge from other individuals – occurs (Brown & Laland, 2003).

23 Joining a group confers many benefits, ranging from predator defence (Magurran, 1990; Stephens &
24 Sutherland, 1999) to improved food location (Pitcher, Magurran, & Winfield, 1982). It is not a

surprise, then, that social groups of fish are very common (Shaw, 1978). Shoaling with individuals that are phenotypically and behaviourally similar is thought to be particularly effective for predator defence due to the oddity effect (Landeau & Terborgh, 1986): individuals that stand out from the group are more likely to be targeted by predators. Consequently, shoals tend to be assorted by size (Croft et al., 2003; Krause & Godin, 1994; Ledesma & McRobert, 2008; Ward & Krause, 2001) and colour (McRobert & Bradner, 1998; Rodgers, Kelley, & Morrell, 2010), in both conspecific and heterospecific contexts (Crook, 1999; Krause, Godin, & Brown, 1996). There are, however, accompanying costs, including increased parasite load (Barber, Hoare, & Krause, 2000) and reduced mating opportunities (Griffiths, 1996). Fish therefore make the decision to associate with other individuals by constant reappraisal of costs and benefits (Pitcher, 1983).

The guppy (*Poecilia reticulata*) has been introduced to every continent with the exception of Antarctica, and is now established in at least 70 countries outside of its native range (Deacon, Ramnarine, & Magurran, 2011). Social behaviour is thought to play an important role in invasion success (Holway & Suarez, 1999) and, as a highly social species, this is may be especially true for the guppy (Deacon & Magurran, 2016). Initial introductions are likely to be just a few individuals , possibly even a single pregnant female (Deacon et al., 2011). Shoaling benefits (e.g., dilution of predation risk and improved foraging efficiency) may be especially critical at this stage of the invasion process. If introduced fish also associate with heterospecifics, they further dilute the predation risk. Any increase in survival and in population growth obtained as a result of social interactions with invaders will also help mitigate Allee effects (Camacho-Cervantes, Garcia, Ojanguren, & Magurran, 2014; Camacho-Cervantes, Ojanguren, Deacon, Ramnarine, & Magurran, 2014)

Prior experience can mediate shoaling decisions in two ways – through previous association such as familiarity, and through shared evolutionary history. Familiarity is the tendency of individuals to associate with those they have previously interacted with (Magurran, Seghers, Shaw, & Carvalho,

1994). Socially familiar shoals benefit from decreased resource competition (Höjesjö, Johnsson, Petersson, & Järvi, 1998) and lower aggression due to the presence of more stable social hierarchies (Johnsson, 1997). This may be due to lower perception of risk or elevated levels of social learning in such assemblages (Morrell et al., 2008). Additionally, higher cohesion (more compactness) is observed in shoals comprised of socially familiar individuals (Chivers, Brown, & Smith, 1995) and produces more effective antipredator behaviour (Mathis & Smith, 1993).

Evolutionary history also shapes behaviour. For example, fish from localities where there are many predators have a higher schooling tendency and stronger evasion behaviours than those from sites where predation risk is reduced (Brown, Macnaughton, Elvidge, Ramnarine, & Godin, 2009; Magurran & Seghers, 1990; O'Steen, Cullum, & Bennett, 2002; Seghers, 1973). Mate discrimination is another behaviour that can be influenced by shared history. In Trinidad, for instance, the guppy is found primarily in freshwater streams, though in certain locations its range extends into the habitat of the phenotypically-similar species, the swamp guppy (*Micropoecilia picta*) which is usually restricted to brackish water (Magurran & Ramnarine, 2004). Consequently, some guppy populations occur sympatrically with *M. picta* (i.e. shared evolutionary history), while other populations do not. Guppies that occur sympatrically with *M. picta* are less likely to attempt interspecific mating – even if they have been reared in single species environments (Magurran & Ramnarine, 2004, 2005).

Here we take advantage of the natural experiment provided by the existence of allopatric and sympatric populations of *P. reticulata* and *M. picta* in Trinidad to examine the shoaling decisions of guppies. In the context of this work, the shared history of guppies that co-occur with *M. picta* involves both evolutionary history and familiarity. Given the well documented advantages enjoyed by conspecific shoals we predict that shoal cohesion will be greatest in single species shoals, as opposed to shoals where two species are present irrespective of the origins of the heterospecific. However, we also expect that if a heterospecific is present, shoal cohesion will be higher when the

fish are derived from populations with a shared history than those for which there has been no prior contact.

METHODS

Experiments were conducted in July and August 2013 at The University of the West Indies.

Fish collection & Ethical Note

Female fish were collected using hand seines from the following locations in Trinidad: (A) Sumaria Trace (guppies and *M. picta*) (B) Cunupia river (guppies and *M. picta*) (C) Caura river (guppies alone) (D) Acono river (guppies alone) (E) Lower Tunapuna (guppies alone) (**Table 1**) and transported to the laboratory in buckets filled with water from the location of capture at densities below 0.5g/L (40 fish per 18L). As collection sites were within 20 minutes driving time from the university, we did not have concerns about temperature or aeration levels causing stress to the fish. At the laboratory, they were sorted by location and placed in single-species aquaria filled with aged tap water at maximum densities of 50 individuals in a tank of dimensions 60 cm long x 30 cm wide x 30 cm high (approximately 1 g per 5L). Fish were allowed time to acclimate to the laboratory conditions and were housed in glass tanks lined with gravel and large stones, which made foraging easy and minimised stress. The lab was illuminated between the hours of 7:00 am and 6:00 pm, in line with the natural photoperiod. Fish were fed to satiation before and after experiments with TetraMin flakes. Tanks were visually isolated from each other using sheets of white paper to limit stress. Water quality was maintained by using sponge filters and performing partial water changes. Our experiments did not involve any invasive sampling or any procedures that would cause pain to fish, and handling times were minimised to limit stress. To further limit stress, tanks were also visually isolated during behavioural trials and only exposed on one side to a single observer, who stayed as still as possible. Fish were housed in the laboratory for no more than 6 weeks and upon completion of experiments, were released into an ornamental pond on The University of the West Indies campus. Guppies were used only once in experiments while some *M. picta* were reused due to low

numbers collected; upon emptying of the three *M. picta* stock tanks, the stock was replenished randomly using fish from the 'used' fish tank. This encompassed the last third of the heterospecific trials (approximately 100 *M. picta*). The probability of using the same three fish (see experiment design below) in any two replicates was extremely low. Furthermore, all *M. picta* treatments had the same number of trials that reused fish, so there was no consistent bias in reusing fish for any one treatment.

Experiments

Six female fish were placed into a 90cm x 30 cm x 30 cm observation tank and allowed to settle for 10 minutes. Females were chosen because they have stronger shoaling tendencies than males (Magurran, 2005). Shoals contained a range of sizes, and the size of the focal fish was recorded as small (17-21mm TL), medium (22-26mm) or large (27-31mm). *M. picta* females were chosen to be in the same size-range as the female guppies. Depending on the treatment, replicates included two sets of 3 guppies, or 3 guppies and 3 *M. picta*, from either the same or different populations. In pilot trials, 10 minutes was found to be the time required for fish to settle and swim normally. This was then used as the time for settling in experimental trials.

One focal guppy was chosen and the species of, and distance to, the nearest neighbour (in guppy body lengths, approximately 3cm) was recorded every 20 seconds for 10 minutes by one of two observers, who viewed the experimental tank from the side. Given that fish change position frequently within a shoal (Krause, 1993; Partridge, 1982; Pitcher, 1973), we believe that the distance from a single focal fish to the nearest neighbour, when measured with high replication and repeated within-trial measurements, captures shoal conformation. Furthermore, the nearest neighbour distance can be accurately scored by eye (Pitcher & Parrish, 1993) and is unlikely to be affected by fish size as our experiments randomised fish size and thus there would be no systematic bias or correlation between fish size and treatment. The presence of mixed shoals, i.e. at least three individuals of different species within 4 body lengths of one another (Pitcher & Parrish, 1993) was

also recorded along with each distance measurement (every 20 seconds). This was repeated for 20 females from each of 5 guppy populations.

Treatments were designed to allow for contrasts between conspecific and heterospecific shoals as well as between heterospecific shoals in which guppies either did or did not possess a shared history with *M. picta* (**Table 2**), while avoiding the introduction of site as a confounding factor. For example, when comparing the response of guppies from site C to guppies from site A or *M. picta* from site A, we did not need to be concerned about the origin of the second three fish affecting our interpretation.

Statistical methods

For each focal guppy in a mixed species trial, the remaining 5 fish consisted of 2 guppies and 3 *M. picta*. Therefore, if shoaling randomly, the focal fish's nearest neighbour should be a guppy 40% of the time. The observed values for all mixed species replicates (20 replicates per treatment for 5 treatments, see Table A1, Supplementary Material) were compared with this expected proportion using a one sample t-test.

Initial investigation of distance data revealed a Poisson-type distribution with a strong positive skew (**Fig. 1**). Simple and generalised linear models with appropriate error structure were unable to provide a good fit to the data. Mixed-effects and generalised mixed-effects models provided better model diagnostics but suffered from convergence problems. A Bayesian generalised linear mixed-effects modelling approach was therefore used instead, via the R package MCMCglmm (Hadfield, 2010). We used a weakly informative inverse-gamma prior and ran models for 1 000 000 iterations with a burn-in of 50 000 and a thinning interval of 100. Separate models were used to examine the effect of the presence of *M. picta* and shared history with *M. picta* on shoal cohesion. Other variables included in both models were observer and focal fish size. A random effect for focal fish identity was included to account for pseudo-replication and over-dispersion in the data. Variation in distance estimates between two observers was accounted for in the model. Density plots and 95%

highest posterior density intervals (which are akin to 95% confidence intervals) were used to interpret significance of terms (Hadfield, 2015). All analyses were carried out using the statistics software, R (R Development Core Team, 2016).

RESULTS

A one sample t-test of combined data for all sites revealed that guppies had a conspecific neighbour significantly more often than expected in mixed species treatments ($t_{99} = 9.798$, $P < 0.001$; data in Table A1, Supplementary Material). This relationship was the same for all five sites (Site A: $t_{19} = 5.293$, $P < 0.0001$; Site B: $t_{19} = 3.434$, $P < 0.01$; Site C: $t_{19} = 6.717$, $P < 0.00001$ $2.026e-06$; Site D: $t_{19} = 3.971$, $P < 0.001$; Site E: $t_{19} = 3.760$, $P < 0.01$). More than 80% of mixed species trials consisted of more than 80% mixed shoals.

MCMCglmm models indicate that neither the presence of a second species, nor shared history, had a significant effect on the nearest neighbour distance. Density plots (**Figs. A1 & A2**, Appendix) and 95% highest posterior density intervals (**Table 3** and **Table 4**) show that the effect of a second species and shared history lie around zero suggesting that these variables are non-significant. Trace plots (**Figs. A1 & A2**, Appendix) show no obvious trends, suggesting that the model ran successfully, and autocorrelation values were all below 0.05. There was a significant observer effect, but our model accounts for this and preserves our interpretation of the data.

DISCUSSION

Our findings show that guppies freely shoal with a phenotypically similar heterospecific and that shoal cohesion is unaffected by the presence of this species, whether or not guppies come from populations that have a shared history with the heterospecific. This consistency in shoaling behaviour in the face of novel social conditions could be an important factor in guppy invasive success.

Mixed shoals

Our results support previous findings that guppies will readily form shoals with *M. picta* (Camacho-Cervantes, Ojanguren, et al., 2014). That is, guppies are more likely to be found in mixed shoals when the alternative is either to be alone or part of a smaller single-species shoal. Earlier work with these species entailed choice experiments, where shoals were held in clear bottles and the time spent with each shoal used to quantify preference (Camacho-Cervantes, Ojanguren, et al., 2014). By observing the focal fish in a free-swimming shoal, our design allowed us to quantify shoal compactness, something not possible with a barrier between the focal fish and other individuals. This enabled us to observe the structuring within a shoal, as well as the focal fish's readiness to shoal with heterospecifics. By better replicating a natural situation, our results add a level of ecological validity to the previous work on these two species. Indeed, we found that guppies more frequently had a conspecific than heterospecific nearest neighbour.

Shared history

Additionally, we find that guppies shoal just as closely with a heterospecific as with a conspecific, whether or not they possess shared history. This is surprising given that social familiarity and genetic relatedness are known rules of guppy shoal assembly (Barbosa, Camacho-Cervantes, & Ojanguren, 2016) and one would expect that shoal cohesion might decrease in the presence of an unfamiliar species. Thus, contrary to expectations, guppies behave as 'friendly' shoal-mates towards *M. picta*, despite evolutionary naivety.

The formation of a sub-shoal

Our results enhance understanding of how shoals are organised in mixed species contexts: Guppies often form mixed shoals where the nearest fish is more likely to be a conspecific (**Fig. 2**), effectively producing a guppy 'sub-shoal' within a heterospecific shoal. This conformation does not appear to depend on shared history. It is possible that guppies may be unable to avoid contact if *M. picta* was shoaling very closely. However, comparison to the guppy-only control suggests that either *M. picta*

individuals shoal in as close proximity to guppies as guppies do to one another, or that guppies make no distinction between conspecifics and *M. picta*.

Explanation and implications

Guppies are known to use visual and olfactory cues in identifying conspecifics (Magurran & Seghers, 1994; Morrell et al., 2008) and can judge their phenotype relative to others (Gasparini, Serena, & Pilastro, 2013; Řežucha & Reichard, 2015). Also, phenotype and social familiarity are both factors influencing decisions to shoal (Barbosa et al., 2016). Consequently, identification of individuals from different populations, or of different species, should not be difficult. Yet males may still attempt to mate with female *M. picta* (Liley, 1966) and in this study females associate with *M. picta* as closely as they would with other guppies.

There are two potential explanations for this. Firstly, it is possible that guppies cannot distinguish themselves from *M. picta*. This is unlikely given that it has been established that visual and chemical cues are important, and may even be so finely tuned that they vary between populations (Brown, Elvidge, Macnaughton, Ramnarine, & Godin, 2010). The alternative explanation is that while they are able to distinguish between *M. picta* and conspecifics, a choice is made to shoal with heterospecifics (either by actively seeking them out, or by choosing not to avoid them) as they are sufficiently phenotypically similar and pose little threat. Investigating whether there is indeed a distinct phenotypic or chemical threshold beyond which shoaling behaviour changes may be an interesting area for future work.

Previous work has shown that learning is important in male guppy mate discrimination between conspecific and *M. picta* females (Haskins & Haskins, 1949; Liley, 1966; Magurran & Ramnarine, 2004). If learning in heterospecific contexts is important in mating decisions, it may also be

important for heterospecific shoaling decisions. However, guppies that had a shared history and thus the opportunity to learn to discriminate *M. picta* showed no difference in shoal cohesion to guppies that were not previously exposed. This suggests that, even when given the opportunity to learn discrimination between conspecifics and *M. picta*, guppies still make the choice to shoal with this heterospecific.

Notwithstanding our findings, preference for a single species vs mixed species shoal cannot be discerned as the present experiment did not offer a direct choice. It is possible that the formation of mixed shoals was due to *M. picta* behaviour, rather than that of the guppies. This would be an interesting line for future investigation - at what shoal size or at what conspecific-heterospecific ratio might single-species shoals be more common? This would shed light on the process of decision making in a social landscape. Even more illuminating will be whether costs and benefits (foraging, parasite load etc.) can be shown to validate these decision thresholds. Further investigation using inter-individual distances and tracking for an entire shoal (e.g. Tang, Wu, Huang, Kuang, & Fu, 2017) may reveal more complicated heterospecific shoal dynamics.

Fish were allowed time to settle into the laboratory setting and the observational tank before trials began, and these two species are commonly found in mixed species shoals in certain Trinidadian streams (Magurran & Ramnarine, 2004) therefore we can assume that these findings are relevant to the wild. We do not believe that size-assortative shoaling (Krause et al., 1996) affected our results as each experimental shoal comprised a range of sizes and the size of the focal fish was not significant in our model. Furthermore, while average guppy and *M. picta* size may differ (Torres-Dowdall, Dargent, Handelsman, Ramnarine, & Ghalambor, 2013) females show indeterminate growth (Magurran, 2005) and these species show a broad overlap in size.

Conclusion

Overall, our findings support the idea that the behaviour of this gregarious invasive species is unaltered by the presence of a heterospecific and that shoaling behaviour is likely a substantive

contributor to the invasive success of guppies. Social learning will presumably be most effective for a species that associates closely with individuals of the other species. Thus, guppies in a new environment can potentially be very effective at exploiting social information (sensu Brown & Laland, 2003) and avoiding Allee effects. Understanding the characteristics that predispose a species to be invasive will require examination of the social and behavioural mechanisms that function in the very early stages of invasion.

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Tables (including legends/headings)

Table 1: Location of field sites where fish were collected

Site	Latitude	Longitude	Guppies present?	<i>M. picta</i> present?
A Sumaria Trace	10.56424	-61.43031	✓	✓
B Cunupia River	10.56156	-61.41769	✓	✓
C Caura River	10.68877	-61.35829	✓	X
D Acono River	10.708	-61.40001	✓	X
E Tunapuna River	10.62496	-61.40709	✓	X

Table 2: Number of replicates for each treatment, in the context of the experimental design.

Hypothesis		Site		Number of replicates
1: Species context	2: Shared history	1 st 3 fish	2 nd 3 fish	
Conspecific shoals	Not applicable to conspecific shoals	A	A	20
		B	B	20
		C	A	20
		D	B	20
		E	B	20
Heterospecific shoals	Shoals with shared history	A	A	20
		B	B	20
	Shoals without shared history	C	A	20
		D	B	20
		E	B	20

The first three fish were always guppies and the second three were either guppies or *M. picta* depending on whether it was a conspecific or heterospecific treatment. Hypotheses: (1) guppies form more compact shoals in conspecific than heterospecific treatments and (2) shoals are least compact in heterospecific treatments where they are naïve to *M. picta*. See Table 1 for key to sites.

Table 3 Results of a Markov Chain Monte Carlo generalised linear mixed effects model including presence of a second species.

	post.mean	l-95% CI	u-95% CI
Intercept	0.350	0.205	0.490
Species 2	0.094	-0.028	0.225
Observer 2	0.181	0.050	0.305
Focal Fish Size - Large	-0.045	-0.193	0.110
Focal Fish Size - Small	0.133	-0.029	0.290

Posterior mean (post.mean) and lower and upper 95% posterior density estimates (l-95% CI and u-95% CI, respectively) from a Markov Chain Monte Carlo generalised linear mixed effects model. (Species 2- presence of a second species).

Table 4 Results of a Markov Chain Monte Carlo generalised linear mixed effects model including shared history.

	post.mean	l-95% CI	u-95% CI
Intercept	0.346	0.205	0.493
Shared history	0.143	-0.031	0.309
No shared history	0.062	-0.085	0.209
Observer 2	0.179	0.0479	0.305
Focal Fish Size - Large	-0.039	-0.191	0.109
Focal Fish Size Small	0.137	-0.018	0.300

Posterior mean (post.mean) and lower and upper 95% posterior density estimates (l-95% CI and u-95% CI, respectively) from a Markov Chain Monte Carlo generalised linear mixed effects model. (SEH-shared evolutionary history).

Table A1: The frequency at which a guppy was found to be the nearest neighbour for all mixed species replicates. G=Guppy, P= *M. Picta*; A-E=sites

Treatment	Replicate	Number of times a guppy is the nearest neighbour	Number of times <i>M. picta</i> is the nearest neighbour	Percent of the time a guppy is the nearest neighbour
GAPA	1	19	11	63.33
	2	17	13	56.67
	3	10	20	33.33
	4	18	12	60.00
	5	16	15	53.33
	6	15	14	50.00
	7	18	12	60.00
	8	18	12	60.00
	9	13	17	43.33
	10	13	17	43.33
	11	17	13	56.67
	12	17	13	56.67
	13	18	12	60.00
	14	11	19	36.67
	15	12	18	40.00
	16	15	15	50.00
	17	19	11	63.33
	18	17	13	56.67
	19	18	12	60.00
	20	10	20	33.33
GBPB	1	17	13	56.67
	2	18	12	60.00
	3	18	12	60.00
	4	18	12	60.00
	5	7	23	23.33
	6	11	19	36.67
	7	15	15	50.00
	8	17	13	56.67
	9	17	13	56.67
	10	11	19	36.67
	11	13	17	43.33
	12	16	14	53.33
	13	17	13	56.67
	14	21	9	70.00
	15	16	14	53.33
	16	14	16	46.67
	17	18	12	60.00

GCPA	18	12	18	40.00
	19	6	24	20.00
	20	18	12	60.00
	1	21	9	70.00
	2	23	7	76.67
	3	26	4	86.67
	4	14	16	46.67
	5	16	14	53.33
	6	9	21	30.00
	7	19	11	63.33
	8	23	7	76.67
	9	18	12	60.00
	10	16	14	53.33
	11	21	9	70.00
	12	21	9	70.00
	13	20	10	66.67
	14	21	9	70.00
	15	18	12	60.00
	16	16	14	53.33
GDPB	17	16	14	53.33
	18	17	13	56.67
	19	17	13	56.67
	20	11	19	36.67
	1	11	19	36.67
	2	14	16	46.67
	3	19	11	63.33
	4	18	12	60.00
	5	14	16	46.67
	6	12	18	40.00
	7	16	14	53.33
	8	18	12	60.00
	9	3	27	10.00
	10	19	11	63.33
	11	12	18	40.00
	12	22	8	73.33
	13	19	11	63.33
	14	20	10	66.67
	15	14	16	46.67
	16	20	10	66.67
GEPB	17	23	7	76.67
	18	12	18	40.00
	19	20	10	66.67
	20	18	12	60.00
	1	10	20	33.33
	2	20	10	66.67
	3	19	11	63.33
	4	17	13	56.67

5	11	19	36.67
6	25	5	83.33
7	19	11	63.33
8	18	12	60.00
9	9	21	30.00
10	23	7	76.67
11	30	0	100.00
12	11	19	36.67
13	19	11	63.33
14	14	16	46.67
15	18	12	60.00
16	9	21	30.00
17	18	12	60.00
18	9	21	30.00
19	18	12	60.00
20	19	11	63.33

Figure Legends (Main text)

Figure 1: Frequency distribution of nearest neighbour distances for all trials combined. (Distance to nearest fish measured in guppy body lengths, ~ 3cm)

Figure 2: A pictorial representation of our results, showing the shoaling behaviour of guppies (blue) and *M. picta* (red). The symbols ✓ and X describe whether guppies have (✓) or do not have (X) shared evolutionary history with *M. picta*. Conformation A (nearest neighbour is a guppy) occurs more frequently than either B or C (nearest neighbour is *M. picta*). The distances to the nearest fish (a, b and c) do not differ between conformations. (to be reproduced in colour)

Appendix

Figure A1: Density curves (left) and trace plots (right) for parameter estimates from a Markov Chain Monte Carlo generalised mixed effects model of shoal cohesion: (a) intercept,

(b) presence of a second species, (c) observer effect, (d) focal fish size (large) and (e) focal fish size (small). Left panel: x-axis: parameter estimate, y-axis: relative density; Right panel: x-axis: number of iterations ($\times 10^3$), y-axis: parameter estimate.

Figure A2: Density curves (left) and trace plots (right) for parameter estimates from a Markov Chain Monte Carlo generalised mixed effects model of shoal cohesion: (a) intercept, (b) shared evolutionary history, (c) no shared evolutionary history, (d) observer effect, (e) focal fish size (large) and (f) focal fish size (small). Left panel: x-axis: parameter estimate, y-axis: relative density; Right panel: x-axis: number of iterations ($\times 10^3$), y-axis: parameter estimate.

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Figure 1
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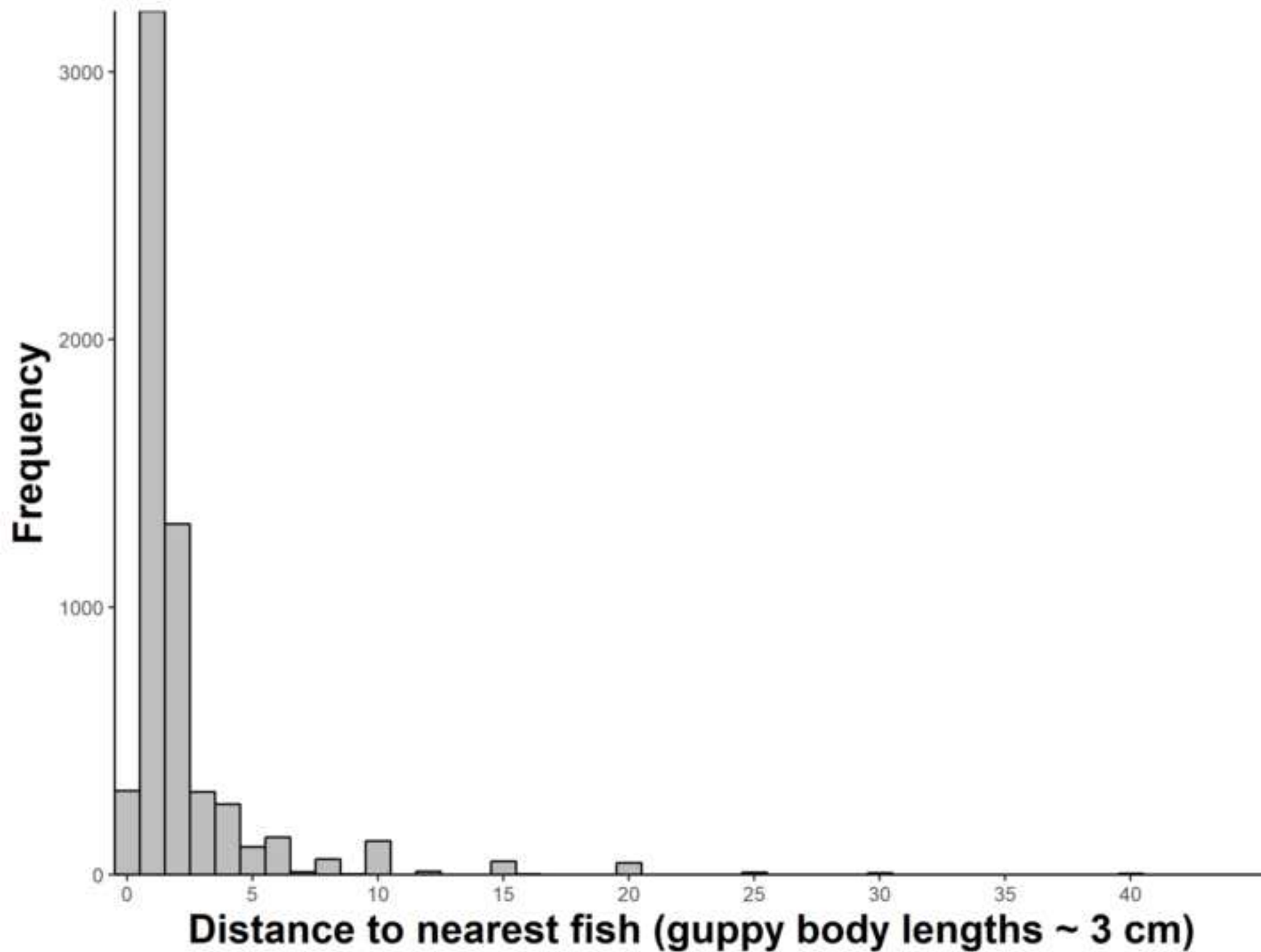


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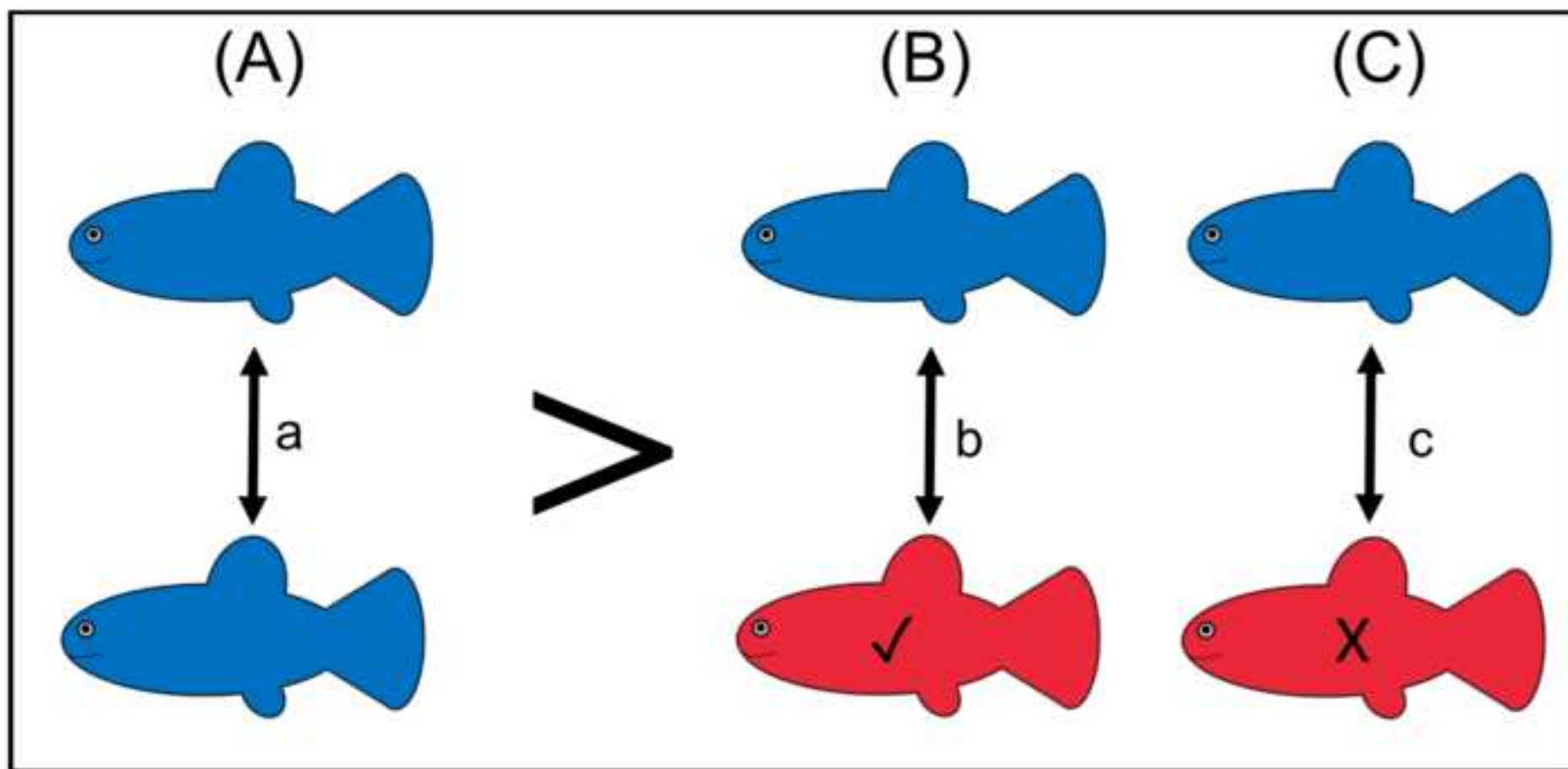


Figure A1
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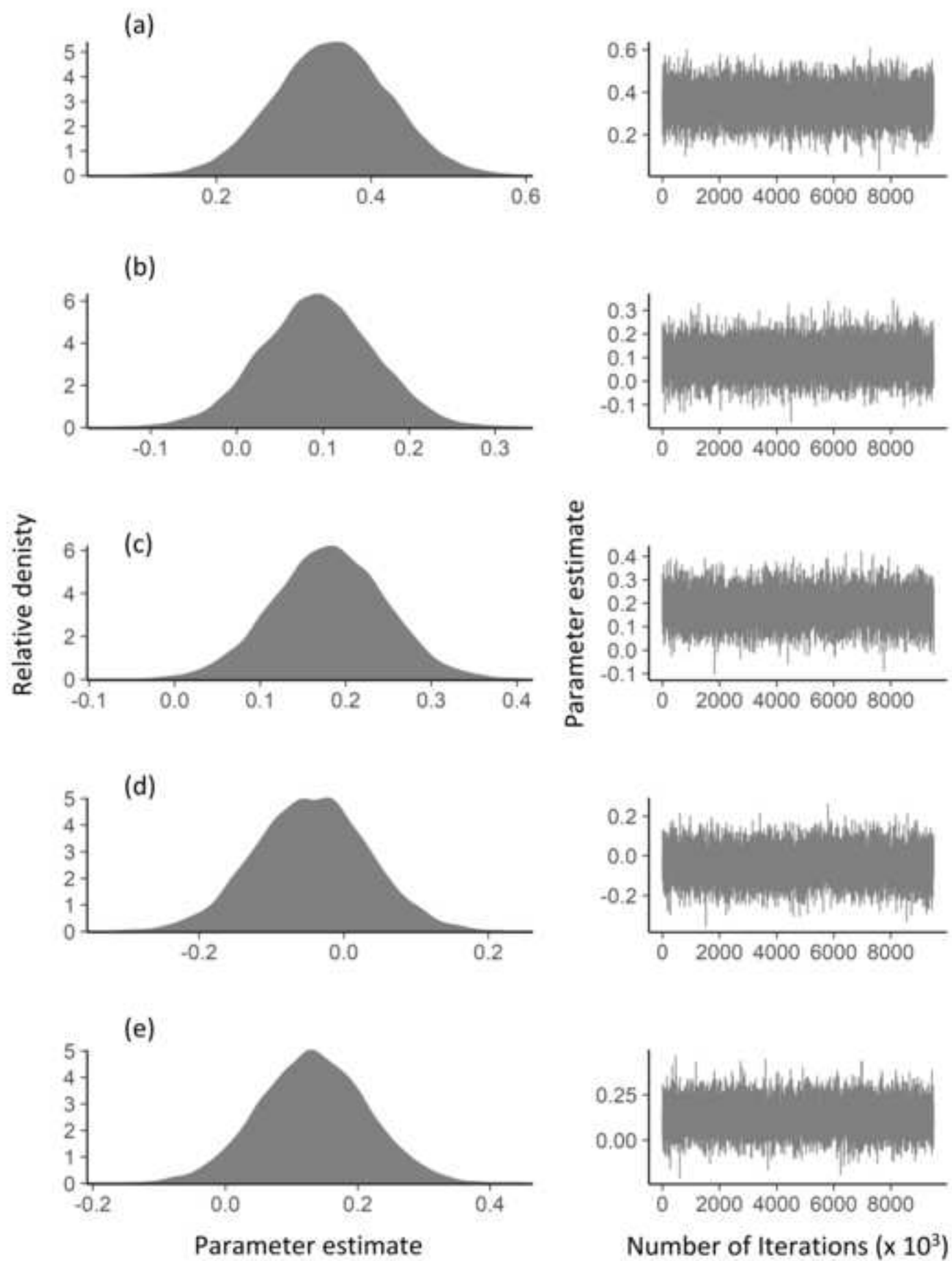


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